RAMSEYOCRINUS AND *RISTNACRINUS* FROM THE ORDOVICIAN OF BRITAIN

by STEPHEN K. DONOVAN

ABSTRACT. *Ramseyocrinus* Bates, 1968, has hitherto been included in the family Eustenocrinidae Ulrich, 1925, but it differs from all other members of this family in having only four radials, an anal X which is supported by two radials (rather than two or three superradials, or a brachianal and superradial), a cup which is about as wide as high, and a column which is tetrameric proximally and tetragonal holomeric distally. A new family, Ramseyocrinidae, is erected for this genus. Of the true eustenocrinids, *Ristnacrinus* Öpik, 1934 is recognized from the British Ordovician for the first time, based upon the occurrence of its distinctive columnals with synarthrial articulating ridges. *Ristnacrinus* columnals are known from four localities of Cautleyan–Rawtheyan (?Hirnantian) age and comparison with similar columnals from the Swedish Boda Limestone (Ashgill) suggests that more than one species may be present in Britain.

ONLY about thirty crinoid species have been described from the British Ordovician (Ramsbottom 1961; Bates 1965, 1968; Brower 1974; Donovan 1983). However, dissociated skeletal elements of crinoids, especially columnals, are common particularly in the Caradoc and Ashgill. Only highly distinctive columnals are of practical use in taxonomy, as homeomorphs between distantly related taxa are probably common (Broadhead and Strimple 1977). However, it is possible to make a generic identification of at least some columnals (Donovan 1983). One of the most distinctive of all columnals found in the Ordovician is that of the dististele of *Ristnacrinus* Öpik, 1934, which has been recognized by a number of subsequent authors (Chauvel and Le Menn 1972, 1979; Chauvel *et al.* 1975; Briskeby 1981; Wright 1983).

The radial plates of the dorsal crinoid cup are defined as those ossicles which are radial in position. Basal plates have an interradial orientation. Some inadunate crinoids possess two radial plates in some or all rays of the cup. Such a compound radial is composed of an inferradial (supported by the basal plates) and a superradial (supported by the associated inferradial). *Ristnacrinus* belongs to the family Eustenocrinidae, whose members possess five compound radials. Re-examination of a second British Ordovician crinoid which was thought to belong to this family, *Ramseyocrinus cambriensis* (Hicks) (Bates 1968), reveals that, despite similarities, it is certainly not a eustenocrinid. This species is therefore included here in a new crinoid family, the Ramseyocrinidae.

Terminology used in this paper follows Moore *et al.* (1968), Ubaghs (1978), and Webster (1974).

SYSTEMATIC PALAEONTOLOGY

Class CRINOIDEA J. S. Miller, 1821
Subclass INADUNATA Wachsmuth and Springer, 1881
Order DISPARIDA Moore and Laudon, 1943
Family RAMSEYOCRINIDAE nov.

Diagnosis. Monocyclic crinoids with a low, cylindrical cup, as wide as the proximal column. Four radials, with an anal X supported by two radials. Basals concealed or absent. Four arms, isotomously branched. Anal X bears at least three further plates in the anal series. Proximal stem quadripartite; distal stem holomeric, tetragonal.

[Palaeontology, Vol. 27, Part 3, 1984, pp. 623–634.]

Discussion. Bates (1968) assigned *R. cambriensis* to the Eustenocrinidae but it differs from other members of this family by having only four non-compound radials, an anal X which is supported by two radials (rather than two or three superradials, or a brachianal and superradial) and a column which is tetrameric proximally while retaining tetragonal symmetry throughout. Differences of the cup plate arrangements are illustrated by text-fig. 1.

In *Eustenocrinus* five basals are apparent and are offset from the radials, all of which are compound (text-fig. 1A). The anal series is supported by the superradials of the B-, C-, and D-rays. The first circlet of primibrachs are fixed to the cup. Only four arms are present. *Ristnacrinus* has basals which are either hidden or absent (text-fig. 1B). The five radials are all compound, each superradial supporting an arm. Ossicles of the anal series are small and are supported by the C- and D-ray superradials, to the left of the C-ray brachial. *Peniculocrinus* (text-fig. 1E) is similar to *Eustenocrinus* but the anal series is supported by a large brachianal in the C-ray (i.e. five arms are present) and the D-ray superradial. The first two circlets of brachials are fixed.

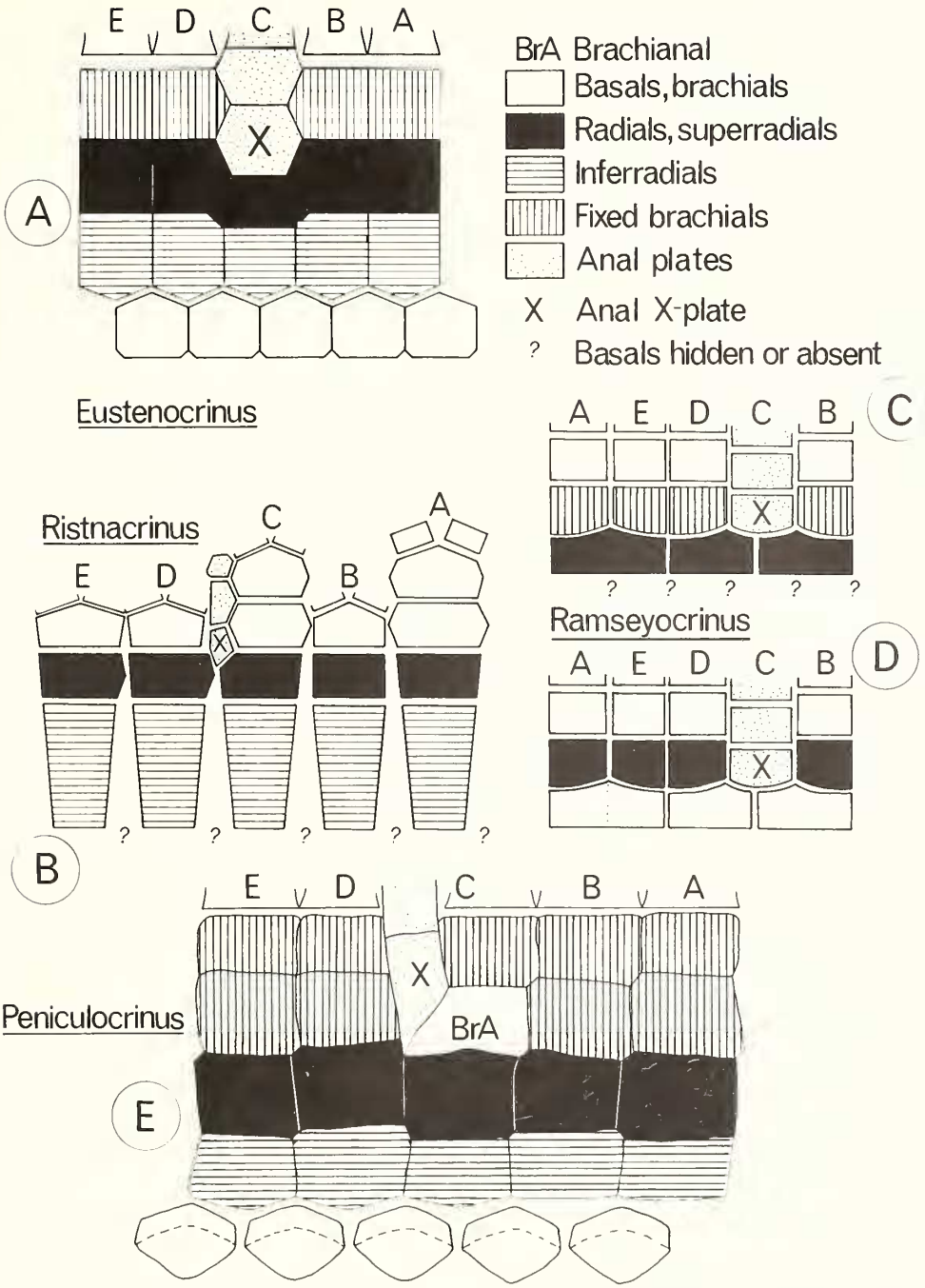
In order to contrast these eustenocrinid genera with *Ramseyocrinus* it is first necessary to define the plates of the cup in the latter. Two alternative interpretations are shown (text-fig. 1C, D). Text-fig. 1D is based mainly upon the interpretation of Bates (1968, p. 407), although his inferradianal is labelled as an anal X. In this plating scheme basals are three in number, the large basal in the A- and E-rays apparently being fused from two smaller plates. Radials are not offset from basals but are directly supported by them. This is unsatisfactory because the 'basals' are radial in orientation. The four arms are directly supported by the radials. The anal X is supported by the two smaller basals.

The interpretation preferred in this paper is shown in text-fig. 1C. Basals are either hidden or absent. The cup is composed of four radials, surmounted by a circlet of four fixed brachials (the ramseyocrinid *Entrochus primus* does not have this circlet of fixed brachials; R. J. Prokop, pers. comm.). The radials in the A- and E-rays are fused. The four arms arise directly from the radials. The anal X is supported by the two smaller radials. This interpretation (text-fig. 1C) is preferred because of the obvious similarities of the cup plating to that of crinoids such as *Eustenocrinus* (although *Ramseyocrinus* does not have split radials, merely radials surmounted by fixed brachials). Radials may be defined as the most proximal plates in each ray (Moore *et al.* 1952, p. 608). It is apparent that the most proximal plates in each ray of *Ramseyocrinus* are those called basals by Bates (1968) (text-fig. 1D). It is therefore correct to regard his 'basals' as radials. Moore *et al.* (1978, p. T554) propose that both basals and split radials are present, i.e. the most proximal circlet of free brachials in text-fig. 1C are incorporated in the cup as superradials, the fixed brachials (this paper) are inferradials and the lowest plate circlet are basals. The first two plates of the anal series are regarded as a compound radial. Similar arguments to those stated above can be applied to show that the lowest plate circlet in the cup is not composed of basals. The lowest free brachial circlet (text-fig. 1C) does not appear to be fixed.

If present, and it is emphasized that this cannot be proved, the basals must be extremely small and are probably concealed by the lobes of the stem. Many articulate crinoids have a hidden circlet of infrabasal plates (cryptodicyclic) (Rasmussen 1978). However, these infrabasals are concealed by relatively broad, circular, or pentagonal columnals. The lobes of the proxistele in *R. cambriensis* are narrow and separated.

The anal tube can be recognized in two specimens of *R. cambriensis* (NMW 29.308.G296 and Manchester Museum L12360). It is also seen in *Entrochus primus* (R. J. Prokop, pers. comm.). In both species the tube is formed of a column of about four plates.

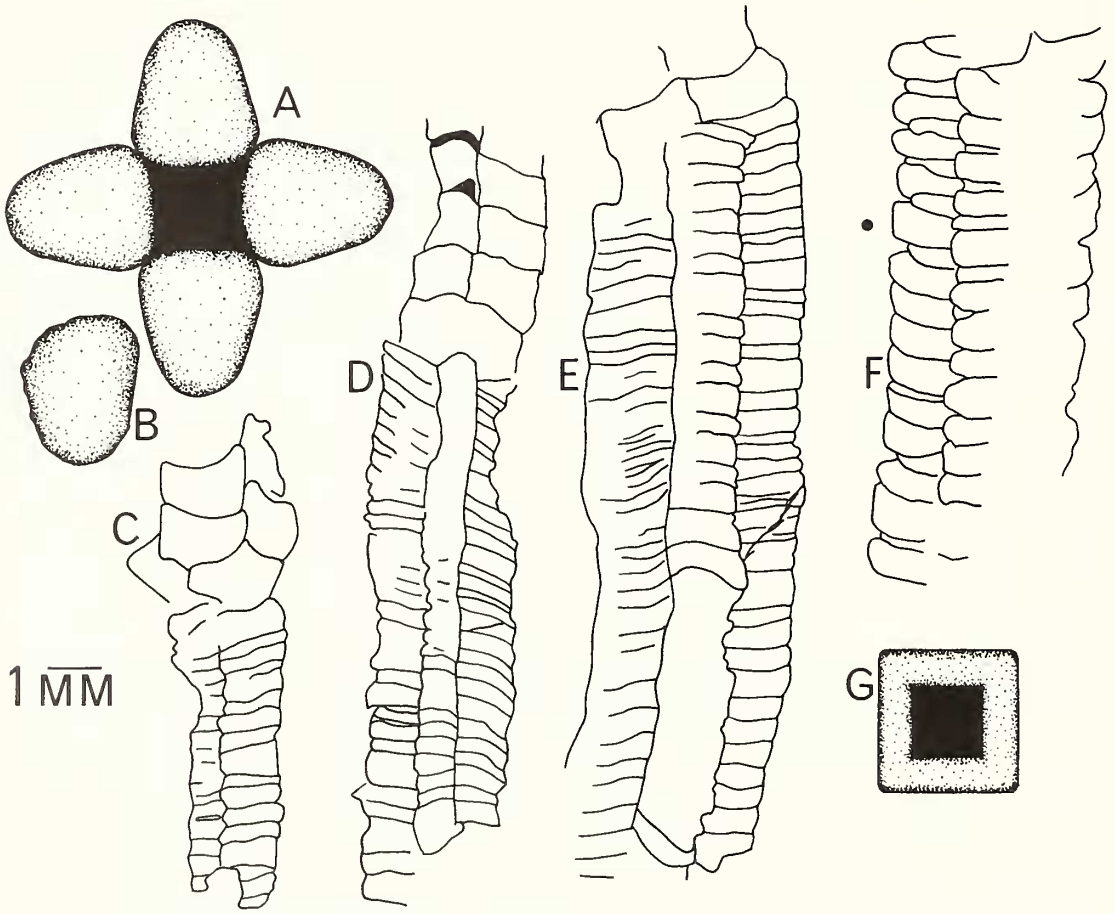
If this new interpretation is now compared with *Eustenocrinus*, *Ristnacrinus*, and *Peniculocrinus*, a number of differences are apparent. Each of the eustenocrinid genera has five compound radials, whereas *Ramseyocrinus* has only four radials, none of which is compound. The cups of eustenocrinids are tall, sometimes incorporating brachials. The cup of *Ramseyocrinus* is about as wide as high, including a circlet of fixed brachials. The anal series of *Ramseyocrinus* is supported by two radials, whereas that in eustenocrinids is supported by three superradials (*Eustenocrinus*), two superradials (*Ristnacrinus*), or a superradial and a fixed brachianal (*Peniculocrinus*). This last point is particularly



TEXT-FIG. 1. Cup plating diagrams for: A, *Eustenocrinus* (after Ulrich 1925; Moore 1962); B, *Ristnacrinus* (after Öpik 1934); C, D, *Ramseyocrinus*. Two interpretations of the cup are shown, both based on NMW 29.308.G296 and G318 (counterparts). In C the basals are hidden or absent, radials and a circlet of fixed brachials are present, and the anal X is supported by two radials (this paper). In D basals and radials are present, two basals supporting the anal X (based on the description of Bates 1968). E, *Peniculocrinus* (after Moore 1962).

important, although it is apparent that minimal reduction of the superradials in the C- and D-rays of *Ristnacrinus* could lead to the anal X being supported by two inferradials.

The stem of *Ramseyocrinus* is also radically different from that of eustenocrinids. The unusual column of *Ristnacrinus* is discussed in detail below but it is sufficient to note here that most columnals are holomeric (i.e. composed of a single ossicle) and circular, with a central synarthrial ridge. *Peniculocrinus* has a subpentagonal column (Moore *et al.* 1978, p. T554), with what appear to be lenticular columnals (cp. Moore *et al.* 1978, text-fig. 347.2e, p. T555, with Taylor 1983, text-fig. 41, p. 61). The stem of *Eustenocrinus* is circular and apparently pentameric (Ulrich 1925, p. 99). The column of *Ramseyocrinus* differs from all these by showing fourfold symmetry (text-figs. 2, 3). The proxistele of *R. caubrieusis* is tetralobate and quadripartite. Distally the column is square but holomeric.



TEXT-FIG. 2. *Ramseyocrinus cambriensis* (Hicks). Columns and columnals. A, reconstruction of the articular facet of a proximal columnal (Donovan 1983, text-fig. 2C). B, NMW 29.308.G220, dissociated mere. C, D, NMW 29.308.G296 and G318 (counterparts), proxistele beneath cup. E, F, BM(NH) E3, proxistele immediately beneath cup (E) and slightly more distal (F, in which the columnal marked by a dot is 36 mm below the base of the cup). G, tentative reconstruction of the articular facet of a distal columnal. Lumen shape, size, and orientation conjectural. All camera lucida drawings of latex casts, except A and G.

Genus RAMSEYOCRINUS Bates, 1968

Type species. Dendrocrinus cambriensis Hicks, 1873, designated by Bates (1968).

Diagnosis. As for the family Ramseyocrinidae, with the first circlet of brachials fixed.

Discussion. The first primibrach circlet of the only other Ramseyocrinid known, *Entrochus primus*, is free above the radials (R. J. Prokop, pers. comm.).

Ramseyocrinus cambriensis (Hicks), 1873

Text-figs. 1C, D, 2, 3

1873 *Dendrocrinus cambriensis* Hicks, p. 51, pl. 4, figs. 17–20.
1960 *Iocrinus? cambriensis* (Hicks) Ramsbottom, pp. 5, 6, pl. 3, figs. 9–11.
1968 *Ramseyocrinus cambriensis* (Hicks) Bates, pp. 406–409, pl. 76, figs. 1–5.

Diagnosis. Radials fused in the A- and E-rays; arms branched isotomously at least four times.

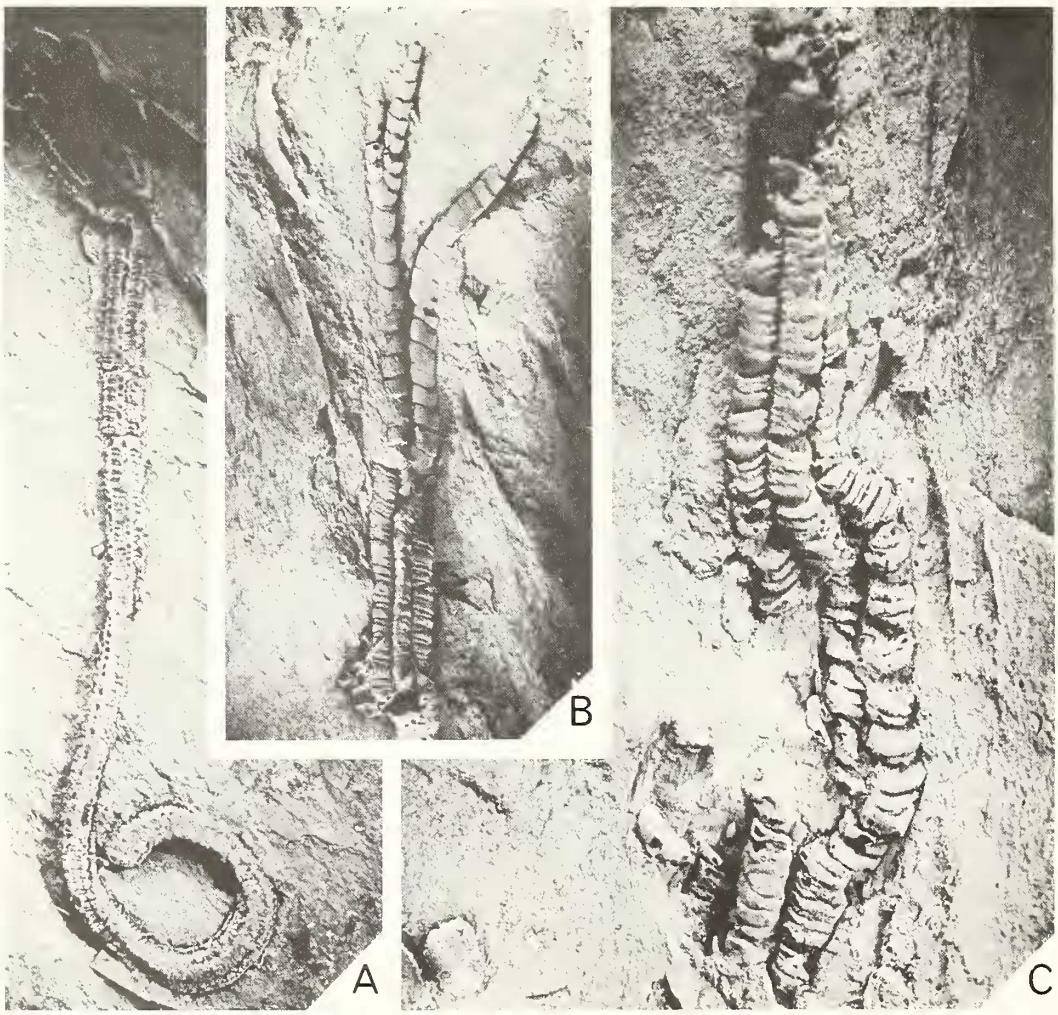
Material. Ramsbottom (1961, p. 5) recognized Sedgwick Museum (SM) A16739 as a syntype (Hicks's fig. 17; also a gutta-percha impression in the Geological Survey Museum collection, IGS GSM 82819) and noted IGS GSM 59428 as a gutta-percha impression of the specimen in Hicks's fig. 20. His description is based mainly on British Museum (Natural History) specimen BM(NH) E3. Bates (1968, p. 407) discovered the counterpart mould of one of Hicks's syntypes (now numbered SM A16739a, b) but based his description on National Museum of Wales (NMW) 29.308.G296 and G318 (counterpart moulds). This description is based on these specimens and also NMW 29.308.G220 and G470(a) (not counterparts), and University College of Wales, Aberystwyth, specimen UCW 21467.

Horizon and Localities. Porth Gain Beds, Ogof Hên Formation (Lower Arenig), Ramsey Island, Dyfed, NGR SM 708 252 (Pringle 1930). Specimens are also known from a quarry on Lleithyr Farm, Dyfed, near to the ruins and by the side of the road to Carnedd, NGR SM 748 248 (Jenkins 1979).

Description. Stem (text-figs. 2, 3A, C) wide proximally, tetrameric, quadrilobate, lobes almost parallel-sided beneath cup, becoming less pronounced distally. Columnals tend to be irregular in height, particularly near the top of the stem (text-fig. 2C–E); diameter of columnals also varies slightly but no more than three orders of columnals are ever present, i.e. two orders of internodal. Articulation synostosial. Lumen tetragonal with inwardly curved sides, angles corresponding to meric sutures (text-fig. 2A). Meres lozenge-like (text-fig. 2B). Distal stem square in section and holomeric; heteromorphic N212 (Webster 1974) but the sequence of internodals is sometimes incomplete. Articulation apparently synostosial (text-fig. 2G). The stem terminates in a planar, coiled holdfast (text-fig. 3A). Basals hidden or absent (text-figs. 1C, D, 3B). Four radials, those in the A- and E-rays fused to form a single large plate (the line of fusion apparent as a groove on NMW 29.308.G318, whereas boundaries between separate plates are clearly evident). Four fixed brachials, two supported by the large radial and one by each of the small radials. Anal X lower than the radials and supported by the two small radials. Anal series of at least four plates of similar morphology. Tegmen not seen. Four arms (text-fig. 3B) supported directly by the four radials. Arms branch isotomously at least four times. At least ten primibrachs, elliptical in section, wider than high, with a narrow, shallow, ventral food groove. Maximum of thirteen secundibrachs, although there may be as few as four (Bates 1968, p. 407); the most proximal three are low, becoming about as wide as high more distally. Tertibrachs higher than wide, ten at most, quadribrachs tall, thin, about twelve, pentibrachs narrow, tall, at least ?five.

Discussion. Only four crinoid genera are known which have a tetrameric column: *Ramseyocrinus*, *Colpodecrinus* (Sprinkle and Kolata 1982; Donovan 1983), *Tetragonocrinus* (Yeltysheva 1964), and *Entrochus* Barrande (previously only known from dissociated columnals but to be fully described from more complete material by Dr. R. J. Prokop). *R. cambriensis* is also the oldest crinoid so far discovered in Britain. The proximal stem is well known from several well-preserved specimens (text-figs. 2A–F, 3B, C). These are all tetralobate and tetrameric, with a random intercalation of internodals often apparent (text-fig. 2C–F).

The columnal morphology has been deduced from NMW 29.308.G220 (text-figs. 2B, 3C). Details of the articular facet are not shown by specimens of 'whole' animals (none is preserved complete with the distal stem) but this specimen is partly disarticulated, enabling the morphology of individual meres to be determined. From this a reconstruction of the facet has been made (text-fig. 2A). The latera of the meres are sub-parallel and it is deduced that the stem fragment is from some distance beneath the cup. The minimal contact between meres of the same columnal did not favour preservation of whole columnals but instead the stem first disarticulated along its meric sutures, producing an effect analogous to peeling the skin from a banana. The separate stem lobes then disarticulated into individual meres.



TEXT-FIG. 3. *Ramseyocrinus cambriensis* (Hicks). A, NMW 29.308.G470(a), dististele with planar, coiled holdfast, ×4. B, NMW 29.308.G318, cup with proximal column and arms, ×3·1. C, NMW 29.308.G220, partially disarticulated stem with a dissociated mere in the bottom left corner, ×3·5. All latex casts whitened with ammonium chloride.

The description of the distal stem is based on NMW 29.308.G470(a) (text-fig. 3A) from Ramsey Island. It cannot be proved that this is *R. cambriensis* but the assumption is based on the absence of evidence for other pelmatozoans at the type locality of the Ogif Hên Formation and the tetragonal symmetry of the specimen. If the assumption is correct, there must have been a change from tetramerism to holomerism distally. The planar coil of the pluricolumnal is suggestive of an attachment structure and is unlike the primitive holdfasts of certain other early crinoids such as *Eclimatocrinus* (Sprinkle 1973) and *Aethocrinus* (Ubaghs 1969). A suggested reconstruction of the articular facet of a columnal of the dististele is shown in text-fig. 2G.

Bates (1968, p. 408) considers *R. cambriensis* to be the most primitive eustenocrinid, possibly closely related to the ancestral stock of the disparids. This may be so but it is unlikely that *Ramseyocrinus* is a direct ancestor of later monocyclic inadunates. It has many unique features not found in later disparids (apart from *Entrochus*), particularly the tetragonal symmetry of the stem and the presence of four arms and radials. Crinoid columnals with fourfold symmetry are not common in the British Ordovician until the Ashgill, when they are more likely to be derived from camerates such as *Xenocrinus* or *Colpodecrinus*.

A final reason for doubting the close relationship of *Ramseyocrinus* to eustenocrinids is stratigraphic. *R. cambriensis* is limited to the Lower Arenig of South Wales, whereas the earliest *Ristnacrinus* columnals are Upper Llandeilo (see below) and both *Eustenocrinus* and *Peniculocrinus* are of Trenton age (mid Caradoc).

Family EUSTENOCRINIDAE Ulrich, 1925

Diagnosis. Monocyclic crinoids with compound radials in all five rays. Basals may or may not be seen. Anal X supported by the B-, C-, and D-ray superradials (*Eustenocrinus*), by the D- and C-ray superradials (*Ristnacrinus*), or by the D-ray superradial and a brachianal in the C-ray (*Peniculocrinus*). Cup conical. Arms isotomously branched. Column round to sub-pentagonal in section.

Genus RISTNACRINUS Öpik, 1934

Type species. Ristnacrinus marinus Öpik, 1934, by original designation.

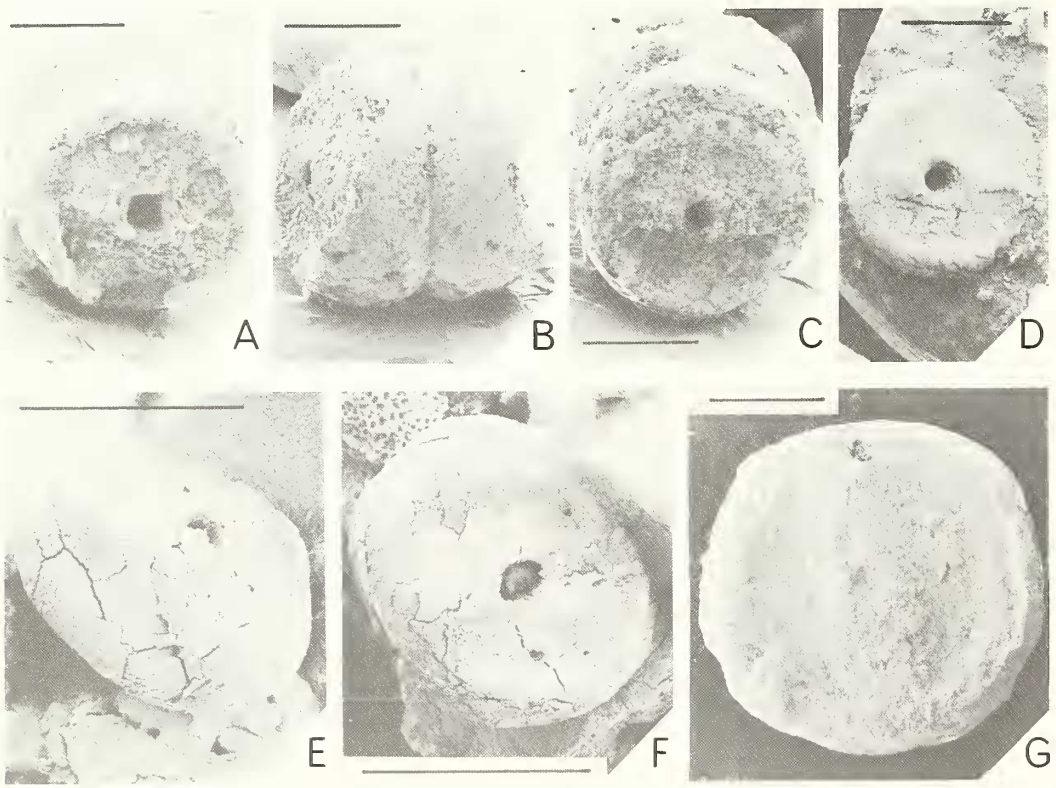
Diagnosis of stem. Stem circular in section; latera convex; proxistele heteromorphic, N1, with symplexially articulated columnals. Articular facet of a distal columnal has a central, synarthrial ridge flanked by two depressed ligament areas which are surrounded by a marginal rim; latera convex.

Discussion. Ristnacrinus, *Caleidocrinus multiramus*, and an undescribed columnal species from the Boda Limestone of Osmundsberget, Sweden, are the only Ordovician crinoids known to have columnals with synarthrial articulation. The latter is elliptical and low (possibly myelodactylid) and the columnals of *C. multiramus* have less convex latera and are proportionally taller than those of *Ristnacrinus*.

The type species of *Ristnacrinus*, *R. marinus*, is founded on a particularly complete specimen, three cups and fragmentary columnals and pluricolumnals from the Caradocian D_1 (Jòhvi) Stage of Estonia (Öpik 1934), which is approximately equivalent to the late Harnagian to early Soudleyan of Britain (Williams *et al.* 1972). The near-complete specimen lacks a distal termination to the column but retains about 35 cm of the stem. This is divided into a short proxistele and a much longer dististele. The proxistele of fifteen columnals is heteromorphic, N1 (Webster 1974), with alternating nodals and internodals with convex and concave latera, respectively. These have a radial symplexial articulation (Öpik 1934, p. 4). The dististele is highly flexible, homeomorphic, and composed of columnals with a synarthrial articulating ridge on each articular facet. Dissociated columnals of this type are easily recognized as belonging to *Ristnacrinus*. Öpik (1934, p. 1) notes that similar columnals are also found below (Kukruse Limestone and Oil Shale, Stages C_2 and C_3, Upper Llandeilo to early Harnagian) and above (Keila Limestone, D_2 Stage, late Soudleyan) the Jòhvi Stage.

D. K. Wright (1983) has noted columnals from the Longvillian and Woolstonian of Snowdonia, North Wales, which are almost certainly *Ristnacrinus* (his *Cyclocyclopa* D). The species *R. cirrifer* Le Menn is based upon dissociated, cirriferous columnals from the Upper Ordovician (Ashgill) of Coat-Carrec, Argol, south-east of Brest, Brittany, France (Chauvel and Le Menn 1972). *Ristnacrinus* cf. *cirrifer* is also known from the Ashgill of Aragon, Spain (Chauvel *et al.* 1975; Chauvel and Le Menn 1979). Briskeby (1981) described columnals of *R. ?marinus* from the Upper Ordovician of Hadeland, north of Oslo, Norway. Finally, columnals of *Ristnacrinus* sp. have been found below the Swedish Kullsberg Limestone (Upper Llandeilo) at Kullsberg, Dalarma, and in the Ashgill Boda Limestone (C. R. C. Paul, pers. comm.).

Synarthrial articulation has evolved three, or perhaps four, times in crinoid columns, in inadunates (ristnacrinids, including *C. multiramus*, and myelodactylids), camerates (platycrinitids), and articulates (bourgueticrinids). The British Ashgill *Ristnacrinus* columnals are similar to those illustrated by Öpik (1934, pl. 1 (labelled pl. 2), fig. 2). One of Öpik's columnals appears to bear some sort of process, possibly a cirrus. If so, this would seem to invalidate *R. cirrifer* Le Menn. Indeed, columnals of this genus show such limited morphological variation, despite their distinctive appearance, that it is here considered expedient to regard them all as *Ristnacrinus* sp.



TEXT-FIG. 4. Scanning electron micrographs of *Ristnacrinus* sp. from the Ashgill of Britain. A–C, BM(NH) E69201. A, C, articular facets at each end of the pluricolumnal; B, lateral view. D, BM(NH) E69202, articular facet. E, F, BM(NH) E69207. E, lateral view; F, articular facet. G, BM(NH) E69199, articular facet. Scale bars represent 1 mm.

Ristnacrinus sp.

Text-figs. 4, 5

Material. Eleven British Museum (Natural History) specimens: BM(NH) E69197 to E69207.

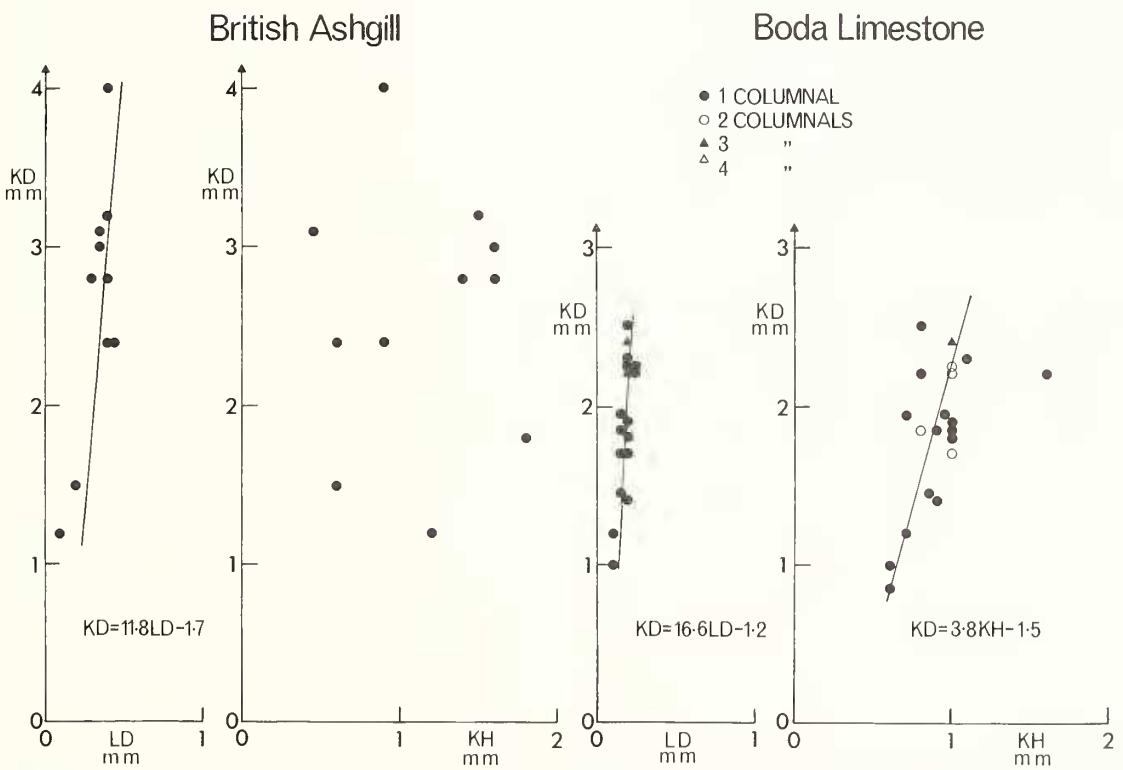
Horizons and Localities. These columnals come from four localities.

(*a*) BM(NH) E69205. At the top of the quarry in the wood, behind the school, Corwen, Clwyd. NGR SJ 071 433. Rawtheyan siltstones. Collected by Mr. B. Cullen.

(*b*) BM(NH) E69206. Loose at the +39·70 to +41·00 m level, west side of Sholeshook railway cutting (Paul 1973, fig. 5, loc. 1/2W), near Haverfordwest, Dyfed. NGR SM 968 171. Sholeshook Limestone. Cautleyan (Price 1973, 1980).

(*c*) BM(NH) E69207. Old factory wall at Ffrydan, near Bala, Gwynedd. NGR SH 922 367. Rhiwlas Limestone. Rawtheyan Zone 5.

(*d*) BM(NH) E69197 to E69204. Keisley Limestone (Upper Ashgill), Keisley, near Appleby, Westmorland. E69202 came from Keisley Bank, above the west quarry, NGR NY 7140 2390 (these are the lowest exposed beds of the Keisley Limestone). E69204 is from the interbedded mudstones and nodular limestones in the north face of Keisley west quarry, NGR NY 7130 2385 (lowest horizons in the quarry). E69198 was *in situ* in the younger limestone horizons of the east face of this quarry. E69197 and E69199 to E69201 come from the east face of the west quarry, where they were washed out from a muddy horizon about 10 m from the top of the section. Finally, E69203 was part of the infill of a trench in the path to the quarry, NGR NY 7135 2380 (A. D. Wright 1982).



TEXT-FIG. 5. KD/LD and KD/KH plots for *Ristnacrinus* sp. from the British Ashgill (*left*) and the Boda Limestone (*right*), where KD = columnal diameter, LD = lumen diameter, and KH = columnal height. Lines of best fit determined by Bartlett's method (Fryer 1966).

Description. Columnal circular to slightly elliptical in outline (cp. text-fig. 4D and 4G with 4F). Lumen circular, central. Axial canal planar-sided. Articular facet traversed by a central, synarthrial articulating ridge which sometimes has a shallow longitudinal groove. In elliptical specimens the articulating ridge lies close to, but not on, the shortest radius (text-fig. 4F). Synarthrial ridge flanked by two large, depressed, semicircular ligament areas. Circumference of the articular facet bordered by a raised rim. Columnals low or barrel-shaped with a convex latus (text-fig. 4B, F). None of the British Ashgill specimens shows an appreciable divergence of the articulating ridges. Columns homeomorphic, although some columnals are apparently wedge-shaped (text-fig. 4B) possibly due to adjacent columnals not resting parallel to each other on their fulcral ridges.

Discussion. Crinoid columnals may be examined by bivariate analysis of suitable parameters (Jeffords and Miller 1968; Roux 1977, 1978; Le Menn 1981). *Ristnacrinus* sp., from the British Ashgill and the Swedish Boda Limestone (Ashgill), have been examined using KD/LD and KD/KH plots (text-fig. 5), where KD = columnals diameter, LD = lumen diameter, and KH = columnal height. The Swedish specimens came from a single horizon and give a very close correlation to lines of 'best fit'. It is probable that only a single species of *Ristnacrinus* is present at this horizon. These columnals seem to differ from the British specimens by showing fulcral ridge divergences of up to about 90°. The British columnals, however, despite having a good KD/LD relationship, generate an apparently random distribution of points on the KD/KH graph. This may be because the columnal height of a single species is highly variable, or it is possibly due to more than one species being represented. As specimens come from four localities, which span the interval Cautleyan to Rawtheyan (Hirnantian?), the latter is most probable. However, it is unlikely that these species could be readily separated without analysing large collections from each of the four localities. These are not readily available, the entire known *Ristnacrinus* fauna from the British Ashgill having been used to produce text-fig. 5.

Acknowledgements. I wish to thank Dr. C. R. C. Paul for critically reading an early draft and loaning specimens of *Ristnacrinus* columnals from the Boda Limestone, Mr. M. Birtle for help in the field at Keisley, Mr. B. Cullen for generously giving me the specimen from Corwen (now BM(NH) E69205), and Mr. C. J. Veltkamp for taking the scanning electron micrographs in text-fig. 4. This work was carried out during the tenure of Natural Environment Research Council research studentship GT4/80/GS/55. Latex casts of *Entroclus primus* were kindly supplied by Dr. Rudolf J. Prokop of the National Museum, Prague, Czechoslovakia.

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Typescript received 6 September 1983
Revised typescript received 14 November 1983